

The effect of overgrazing on the small mammals in Umfolozi Game Reserve

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Abstract

Four trapping grids in two open woodland communities were monitored from July 1982 to December 1983. Small mammal population numbers showed a positive response to a decrease in large ungulate grazing pressure. Diversity indexes of the small mammal community varied with woodland type and ungulate grazing pressure. Certain factors suggested that the quantity of cover is of prime importance to the density and diversity of small mammals but when cover reached threshold levels the degree of plant species diversity became important. Disparate vegetation recovery after rain indicated that small mammals respond to cover improvement rather than rain itself.

Recruitment and breeding condition seemed to be inhibited by the effects of overgrazing. Each sex of *Praomys natalensis*, *Saccostomus campestris*, and *Aethomys chrysophilus* was similarly affected by the impact of overgrazing. Long term recapture rates were higher in zones with less grazing and more cover. The average distance between captures of *P. natalensis* in the overgrazed areas was relatively greater than in regions with reduced grazing pressure while that of *S. campestris* seemed unaffected by cover condition. Mobility of *P. natalensis* was probably influenced by an interaction of small mammal density and cover condition. The 1982/3 drought caused population densities of small mammals throughout the study area to „crash“.

Introduction

Grazing by large herbivores influences many aspects of grassland ecosystems including vertical structure, plant species composition and diversity, and standing crop of plant biomass. The impact on the grass and forb layer, or herb layer, by wild grazing ungulates in their natural habitats has been investigated by numerous workers.

McNAUGHTON (1976) showed that over a four-day period the grazing of migrant wildebeest reduced green biomass by 84.9 % and grass height by 56.0 %. EMSLIE (1982) reported that at Umfolozi Game Reserve (UGR) the standing biomass of the herb layer in a heavily grazed area of *Acacia nigrescens* open woodland was 20.0 % that of a paired site with about half the grazing ungulate stocking level.

EMSLIE 1983 (pers. comm.) recorded 33 % of the offtake of *Panicum coloratum* (Graminae) and 23 % of the offtake of *Themeda triandra* (Graminae) could be accounted for by insects in the non-cull block in 1981–82. He further estimated that between 35 and 40 % of the total grazing occurring in UGR in 1981–82 was by invertebrates. During the drought in 1982–83 harvester termites were the major grazers over large areas in the non-cull block.

DELANY (1964) noted that the species and biomass of small rodents varied with the extent of large mammal grazing. In the savanna of the Crater area (Uganda), with little grazing by large mammals, nine species of small mammals were recorded. A few miles distant at Mweya Peninsula where grazing by buffalo and elephant was extensive only four rodent species were recorded. The rodent biomass in the latter region was only about one quarter of the former.

FRENCH et al. (1976) and GRANT and BIRNEY (1979) have related the importance of the density of above-ground plant biomass to small mammals abundance and distribution.

GRANT et al. (1982) showed that grazing had a direct effect on the structure and productivity of small mammal communities.

Grazers, both vertebrate and invertebrate, can modify the herb layer in terms of structure and species composition to a level where small mammals are affected. Overutilisation of the herb layer by grazers may influence small mammal dynamics in many ways, shelter and food supply are reduced by cover removal while exposure to predation is enhanced.

The aim of this project was to determine the impact of overgrazing on small mammals in UGR.

Study area

UGR (28° 12' to 28° 26' S, 31° 42' to 31° 59' E) covers an area of 47753 ha; two large valleys, sculptured by the Black and White Umfolozi rivers, dominate the undulating topography. Altitudes range from 45–579 m a.s.l. The mean annual rainfall (averaged over 24y) is 680 mm with the wettest months occurring between October and March, although heavy rains sometimes fall in winter. Mist, frost and hail are rare while heavy dew is experienced mainly in autumn and winter (BOURQUIN et al. 1971).

The vegetation in UGR comprises mainly *Acacia* woodland dominated by *Acacia nigrescens*, *A. tortilis*, *A. nilotica*, and *A. karroo* open woodlands. Riparian forest, characterised by *Ficus sycomorus* and *A. robusta*, is confined to drainage lines. Closed woodland is usually found on flat, low-lying areas and is characterised by *Spirostachys africana*. The area falls within the Zululand Thornveld subcategory of the Coastal Tropical

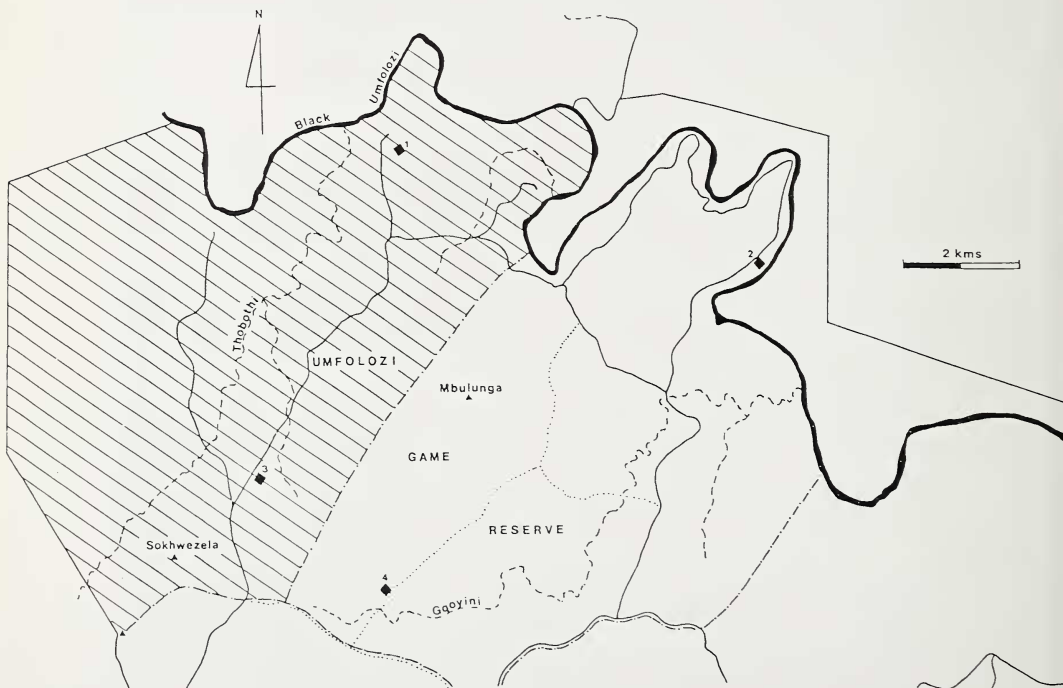


Fig. 1. A map of the bi-zonal study area in Umfolozi Game Reserve showing the locations of the trapping grids (1 = *A. nigrescens* non-cull zone, 2 = *A. nigrescens* cull zone, 3 = *A. tortilis* non-cull zone, 4 = *A. tortilis* cull zone)

Forest types, and the Lowveld subcategory of the Tropical Bush and Savanna types of ACOCKS (1975).

The study area in the northwestern corner of UGR (Fig. 1) was established for research studies, in particular to test vegetation monitoring techniques. The cull and non-cull zones of the study area provided differing environmental conditions through different ungulate stocking levels. In the cull zone stocking levels of grazing ungulates were reduced to about 50.0 % of the carrying capacity (i.e. to an estimated 9.4 AU/100 ha, where one animal unit (1 AU) = ungulate biomass consuming the same amount of energy as a steer weighing 450 kg, e.g. 6.1 impala = 1.8 zebra = 1 AU) while in the non-cull zone there was no ungulate removal. Advantage was taken of the differing environmental conditions, provided by the cull and non-cull arrangement, to assess the impact of overgrazing on small mammal community ecology.

Materials and methods

Trapping was conducted on 10 × 10 grids with PVC live traps (WILLAN 1978) set at 15 m intervals. A trap was usually placed in the most likely site within one metre of the trap station; the 100 traps in each grid were checked daily in the early morning, rebaited and reset. Each trapping session lasted four consecutive nights thereby giving 400 trapnights per session. Bait comprised a mixture of equal parts rolled oats and peanut butter.

Species, weight, sex, and location on the grid, to facilitate calculation of average distance between captures, were recorded for animals captured. The following criteria were used to evaluate reproductive condition: for females, the state of the vaginal opening (perforate or imperforate) and the condition of the nipples (small, enlarged, lactating); and for males, the position of the testes (scrotal or abdominal). Each animal was individually marked using a toe-clip code before being released at its capture site.

Animals were assigned to age-classes (adult, sub-adult, or juvenile) using body mass as shown in Table 1. The lower limit of the adult class was calculated by subtracting one standard deviation from the mean weight of scrotal or perforate adults, to accommodate animals in an emaciated condition caused by the drought. The average distance between captures of individuals was used to assess the mobility of each species.

Table 1. Weight categories used to determine age classes of four rodent species

Species	Females			Males		
	adult (g)	sub-adult (g)	juvenile (g)	adult (g)	sub-adult (g)	juvenile (g)
<i>Praomys natalensis</i>	> 33	21–33	< 21	> 31	21–31	< 21
<i>Saccostomus campestris</i>	> 36	21–36	< 21	> 41	21–41	< 21
<i>Aethomys chrysophilus</i>	> 63	31–63	< 31	> 71	31–71	< 31
<i>Lemniscomys griselda</i>	> 47	21–47	< 21	> 64	21–64	< 21

Small mammal populations were estimated using a weighted mean mark-recapture formula (BEGON 1979):

$$\hat{N} = \frac{M_i \times n_i}{(\Sigma m_i + 1)}$$

where \hat{N} = estimate of the population; M_i = number of marked individuals at risk on day i ; m_i = number of marked individuals caught on day i ; n_i = number of individuals caught on day i .

An index of species diversity was calculated using the following formula (SHANNON 1948):

$$H = \frac{n \log n - \sum f_i \log f_i}{n}$$

where H = species diversity; f_i = number of individuals of one species caught during the trapping session; n = total number of individuals of all species caught during the trapping session.

After exploratory trapping in the study area, two pairs (cull zone vs non-cull zone) of permanent grids were sited in two major vegetation communities viz. *A. nigrescens* and *A. tortilis* open woodlands (Fig. 1).

Data relating to cover was obtained from two sources. First, the species composition and standing biomass of the herb layer was measured by EMSLIE (1982) in April 1982. These data were used to calculate the diversity indexes (Shannon 1948) of the herb layer in each trapping grid. Second, a disc pasture meter (BRANSBY and TANTON 1977) was used to measure the difference in mean height of the forb layer under *A. tortilis* in the two zones in December 1983.

Results

Trapping results (July 1982–December 1983) are given in Table 2, where population estimates indicate a positive response of small mammal densities to reduced grazing ungulate stocking levels in the *A. nigrescens* open woodland until the population crash caused by the drought. The trend in the *A. tortilis* community is unclear; the small mammal community in both the cull and the non-cull zone responded similarly to the prevalent environmental conditions (ungulate stocking levels and low rainfall).

The diversity indexes and standing biomasses of the herb layer in the four study plots are presented in Table 3. These data show that the herb layer diversity was significantly greater in the non-cull than in the cull areas in both *Acacia* communities and that the herb layer under *A. tortilis* was more diverse than that under *A. nigrescens* though significantly so only in the non-cull zone.

The diversity indexes of the small mammal communities in the *A. nigrescens* woodland were higher, though not always significantly so, in the cull zone than the non-cull zone.

Table 2. Small mammal captures, populations estimates (PE), and diversity indexes (DI) in each study grid in Umfolozi Game Reserve from July 1982 to December 1983

Grid Location	Month	Total captures	PE Animals/ha	DI
<i>A. nigrescens</i> :				
Non-cull	Jul	0	0	—
	Oct	4	0.7	.3
	Nov	3	0.8	.3
	Feb	6	1.7	.4
	Apr	5	2.0	.2
	Oct	1	0	—
Cull	Jul	33	10.7	.4
	Oct	16	6.1	.4
	Nov	11	3.7	.4
	Feb	4	1.5	.3
	Apr	3	0.9	.3
	Oct	0	0	—
<i>A. tortilis</i> :				
Non-cull	Jul	9	3.1	.4
	Oct	32	10.7	.4
	Nov	14	4.6	.4
	Feb	9	3.3	.3
	Apr	19	7.7	.3
	Oct	1	0.3	—
	Dec	2	0.4	—
Cull	Jul	22	8.5	.2
	Oct	28	9.8	.1
	Nov	9	3.2	.2
	Feb	6	2.1	.3
	Apr	15	5.4	.3
	Oct	0	0	—
	Dec	7	6.3	.4

Table 3. Standing biomasses (from Emslie 1982) and diversity indexes (which are compared, Hutcheson 1970) of the herb layer in the cull and non-cull zones of *A. nigrescens* and *A. tortilis* open woodlands

		Non-cull	Cull
<i>A. nigrescens</i>	standing biomass g/m ²	220	1005
	(per EMSLIE 1982)		
	diversity index (H)	0.95	0.52
	t		15.7
<i>A. tortilis</i>	v		651
	p		< 0.001*
	standing biomass g/m ²	330	445
	(per EMSLIE 1982)		
<i>A. nigrescens</i> vs <i>A. tortilis</i>	diversity index (H)	1.0	0.78
	t		6.93
	v		758
	p		< 0.001*
<i>A. nigrescens</i> vs <i>A. tortilis</i>	t	-8.34	1.78
	v	945	521
	p	< 0.001*	> 0.05

* Difference significant (at $p < 0.05$).

Table 4. Species caught, total captures, and a comparison (HUTCHESON 1970) of small mammal diversity indexes in the cull (c) and non-cull (nc) zones in two woodland types during July, October and November 1982

	Jul		<i>A. nigrescens</i>		Nov		Jul		<i>A. tortilis</i>		Nov	
	nc	c	nc	c	nc	c	nc	c	nc	c	nc	c
<i>P. natalensis</i>	—	22	2	11	2	8	4	20	24	26	6	8
<i>S. campestris</i>	—	1	2	3	—	1	4	1	3	2	7	1
<i>A. chrysophilus</i>	—	2	—	1	—	1	1	—	4	—	—	—
<i>M. minutoides</i>	—	1	—	—	1	—	—	1	1	—	1	—
<i>C. hirta</i>	—	7	—	1	—	1	—	—	—	—	—	—
Total captures	0	33	4	16	3	11	9	22	32	28	14	9
DI =	—	0.43	0.3	0.4	0.28	0.38	0.42	0.16	0.35	0.11	0.39	0.15
t =	—	—	—1.07	—	—0.68	—	2.56	—	2.69	—	2.18	—
v =	—	—	16	—	13	—	30	—	58	—	15	—
p	—	—	> 0.2	—	> 0.5	—	< 0.02*	—	< 0.02*	—	< 0.05*	—

* Difference significant.

Conversely, the small mammal diversity in the *A. tortilis* cull zone was significantly lower than the non-cull zone (Table 4). Small mammal diversity in the *A. nigrescens* cull zone was significantly higher than the *A. tortilis* cull zone (Table 5).

A comparison of age-structures in the cull and non-cull rodent populations in winter (May and July) and early summer (October and November) showed reduced recruitment in the non-cull zones (Table 6). A clear trend, notwithstanding the small sample sizes, indicates a higher ratio of breeding to non-breeding *P. natalensis* adults in the cull zone. The sex ratios of *P. natalensis*, *S. campestris*, and *A. chrysophilus* were unaffected by overgrazing; analysis showed no significant differences between the cull and non-cull zones (*P. natalensis* $p > 0.1$; *A. chrysophilus* $p > 0.98$; *S. campestris* $p > 0.98$).

Table 5. A comparison of small mammal diversity indexes (HUTCHESON 1970) in the cull zone of *A. nigrescens* (*A. nig.*) and *A. tortilis* (*A. tor.*) open woodlands during July, October, and November 1982

	July		October		November	
	<i>A. nig.</i>	<i>A. tor.</i>	<i>A. nig.</i>	<i>A. tor.</i>	<i>A. nig.</i>	<i>A. tor.</i>
Diversity index (from Table 4)	0.43	0.16	0.40	0.11	0.38	0.15
t	2.534		2.685		1.495	
v	50		27		20	
p	< 0.02*		< 0.02*		> 0.1	
* Difference significant.						

Table 6. A comparison (G-test, SOKAL and ROHLF 1981) of the winter and summer age structures of *P. natalensis* in the cull and non-cull zones (ratio = ratio of adults to sub-adults and juveniles)

		Non-cull		Cull	
		n	ratio	n	ratio
Winter:	adult	3	1.0	9	1.0
	sub-adult	3	1.0	38	4.2
	juvenile	2	0.7	18	2.0
	total	8		65	
	G =				19.51
	p				< 0.001
Summer:	adult	19	1.0	21	1.0
	sub-adult	12	0.6	23	1.1
	juvenile	0	0	6	0.3
	total	31		50	
					*
* Zero frequencies precluded statistical tests.					

Table 7. A comparison (t-test) of the mean distance between captures of *P. natalensis* and *S. campestris* in the cull and non-cull zones over the period July 1982 to April 1983

Species	n	Cull		n	Non-cull		t	df	p
		mean distance (m)	SE		mean distance (m)	SE			
<i>P. natalensis</i>	52	26.42	2.1	36	36.12	3.7	-2.45	86	< 0.02
<i>S. campestris</i>	7	45.1	9.7	6	34.5	12.6	0.67	11	> 0.5

Table 8. Recapture rates of all rodent species marked in July and October 1982

			Jul	Oct	Nov	Feb	Apr	Oct
July:	Cull	n	44	16	5	2	2	0
		%		36.4	11.4	4.6	4.6	
	Non-cull	n	9	6	2	0	0	0
		%		66.7	22.2			
October:	Cull	n		41	8	3	3	0
		%			19.5	7.3	7.3	
	Non-cull	n		33	6	2	1	0
		%			18.2	6.1	3.0	

The average distance between captures of *P. natalensis* was significantly greater in the non-cull zone than in the cull zone while that of *S. campestris* showed no significant difference between zones (Table 7). Long term recapture rates, an indication of survival, were higher in the cull zones (Table 8).

Pasture disc height measurements in the two zones of *A. tortilis* woodland in December 1983, after good spring rains, showed more herb layer in the cull zone (Table 9).

Discussion

BROOKS (1981) calculated that in the study area grazing ungulate stocking levels in April 1982 were 9.4 AU/100 ha in the cull zone and 17.5 AU/100 ha in the non-cull zone. EMSLIE (1982) in his estimations of herb layer standing biomass in *A. nigrescens* and *A. tortilis* open woodlands in the same area (Table 3) showed clearly more vegetation in the cull zone as a result of the reduced stocking levels.

The ramifications of lower stocking levels and subsequent cover improvement on the small mammal community were reflected in the trapping results. In the *A. nigrescens* open woodland the population estimates and diversity indexes are much higher in the cull zone, with significantly more cover, than in the non-cull zone (Fig. 2, Table 2). The relatively

Table 9. Comparison (t-test) of herb layer heights in the cull and non-cull zones of *A. tortilis* open woodland in December 1983

Height class cm	Cull	Non-cull
21-25	2	
16-20	5	
11-15	5	
6-10	44	2
1-5	79	76
0	0	2
n =	135	80
x (cm)	6.15	2.79
SE	0.33	0.14
t =		7.54
Df =		213
p		<0.001

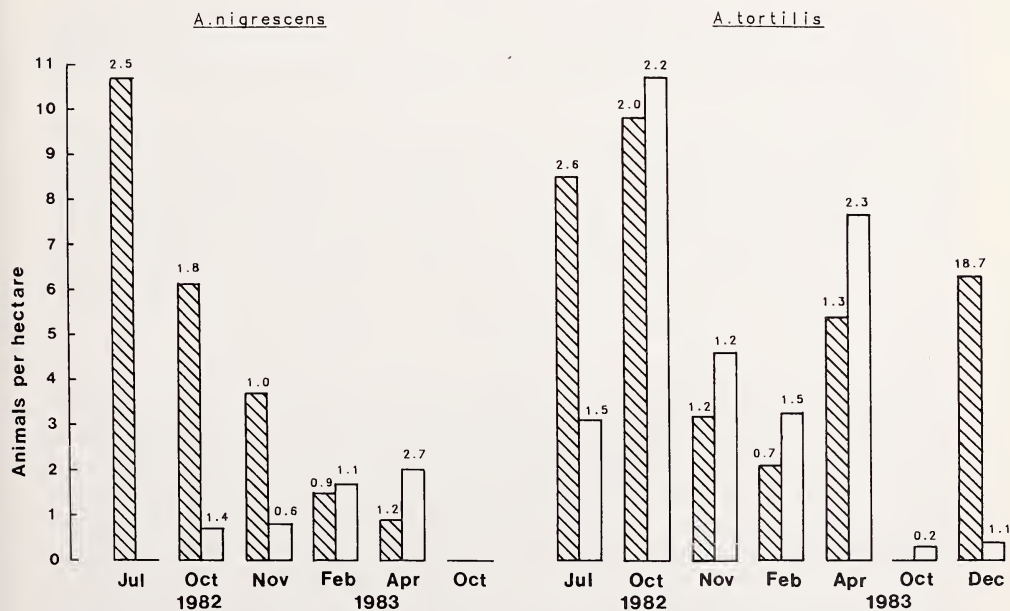


Fig. 2. Population density estimates on the cull and non-cull grids in *A. nigrescens* and *A. tortilis* open woodlands, standard error given above each histogram (▨ = cull zone, □ = non-cull zone)

smaller inter-zonal disparity in standing biomass of the herb layer in *A. tortilis* open woodland probably accounts for the generally similar small mammal population densities.

GRANT et al. (1982) found that a reduction in cover in tall-grass grasslands resulted in a decrease in total rodent biomass and suggested some site-specific threshold at which cover is no longer sufficient to support a dense small mammal population. Reduction in vegetative cover in the overgrazed non-cull zone may have brought cover level to or below this threshold level. Small mammal population density estimates on the *A. nigrescens* non-cull grid indicated that cover (standing plant biomass = 220 g/m²; EMSLIE 1982; Table 3) was probably below the threshold level whereas in both *A. tortilis* zones (standing biomass = 330 g/m² – non-cull and 445 g/m² – cull; EMSLIE 1982; Table 3) cover may have been at or just above threshold levels. Cover in the *A. nigrescens* cull zone most probably exceeded the threshold level by a comfortable margin which facilitated high small mammal densities before the onset of the drought.

MC'CLOSKEY (1976) reported that in coastal sage scrub in southern California vegetation structure was important in determining small mammal community composition while GRANT et al. (1982) found that in four types of north American grasslands the structural characteristics of the grass community were more important than the plant species composition of the small mammal community. DELANY (1972) provides evidence that small mammal populations and biomass can vary considerably from one grassland type to another, even within different types of woodland savanna; and that greater vegetational heterogeneity is related to a more diverse fauna.

The diversity of the herb layer, measured in terms of species contribution to standing biomass, was significantly greater in the non-cull zones of both woodland communities. The small mammal diversity in the *A. nigrescens* open woodland was greater in the cull zone with its substantial, though less diverse, grass cover. The *A. tortilis* open woodland, with relatively less cover, accommodated a more diverse small mammal community in the vegetatively more diverse non-cull zone. However, the cull zone of the *A. nigrescens* open woodland supported a more diverse small mammal community than that of *A. tortilis* open woodland notwithstanding a more diverse grass community in the latter. These factors suggest that cover quantity is of prime importance to the density and diversity of small mammals but with cover at threshold levels the degree of plant species diversity becomes important.

The response of the herb layer to above average rainfall in October and November 1983 differed in the two zones, in December the mean grass height in the *A. tortilis* non-cull zone was 28 mm while in the cull zone it was significantly higher at 62 mm. Ungulate grazing pressure most probably accounted for the disparate vegetation recovery. By October 1983 all rodent communities were virtually obliterated by drought yet in December some recovery was evident in the *A. tortilis* cull zone (6.3 vs 0.4 animals/ha). That small mammal resurgence was evident only in the zone of substantial cover regeneration suggests that they responded to improved cover conditions rather than the rainfall itself.

Recruitment was inhibited by overgrazing and resultant cover degradation. In winter and summer the proportion of sub-adults and juveniles present in the population is greater in the cull zone than in the non-cull zone. Poor recruitment rate may stem from, firstly, a reduction in fecundity of the adults and, secondly, the juveniles being vulnerable to the harsher conditions (less food, greater exposure to predators and/or climatic extremes) in the non-cull zone. The ratio of breeding to non-breeding adults at the height of breeding season (Oct.–Feb.) is higher in the cull zone. Either the adverse conditions trigger a reproductive inhibitor in the animals or the degraded vegetation precludes an environmental reproductive stimulant. DELANY (1972) suggested that the onset and termination of breeding could be correlated with biochemical and quantitative changes in the diet while SANDERS et al. (1981) found that the reproductive condition in *Microtus montanus* was

initiated by the intake of green shoots containing a cyclic carbamate (6MBOA). In this study heavy grazing pressure by large ungulates would have denied new shoot availability to small mammals thereby inhibiting reproduction.

The greater average distance between captures of *P. natalensis* in the non-cull zone with reduced cover, depleted food resources and lower small mammal densities indicated that mobility may be influenced by an interaction of these factors. The animal has to forage further afield to satisfy basic needs and is allowed to do so because small mammal populations are sparse. The average distance between captures of *S. campestris* was similar in both zones. This animal has a wide habitat tolerance, from sandy open veld, dense bush to forests (DE GRAAFF 1981), and so it is likely that its mobility would be more influenced by food availability and predation than cover condition alone.

The importance of cover to the small mammal community is again emphasised by the greater survival rates, as indicated by long term recapture rates, in the cull zones. Environmental stress on the animals is intensified by cover degradation in terms of food and shelter reduction and increased predation and probably results in decreased longevity.

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Zusammenfassung

Die Auswirkungen von Überweidung auf Kleinsäuger im Umfolozi-Wildpark

Die Kleinsäugerpopulationen im Umfolozi-Wildpark in Südafrika wurden auf vier Probeflächen mit Fallengittern von Juli 1982 bis Dezember 1983 verfolgt. Verglichen wurden Savannen mit *Acacia nigrescens* und *A. tortilis* in Gebieten mit hoher Dichte großer Pflanzenfresser mit solchen Gebieten, in denen der Einfluß der Weidetiere auf die Hälfte reduziert war. In den weniger beweideten Gebieten waren Dichte und Diversität der Kleinsäuger höher als in den stark beweideten. Ferner war in den weniger beweideten Regionen der Anteil von Jungtieren höher und die durch Wiederfang geschätzte Lebenserwartung der Nager größer. Dagegen ergaben sich keine Nachweise für Unterschiede im Geschlechterverhältnis auf Flächen mit üppiger und spärlicher Vegetation bei den untersuchten Arten *Praomys natalensis*, *Saccostomus campestris* und *Aethomys chrysophilus*. Der mittlere Abstand mehrfach gefangener *Praomys natalensis* zwischen zwei Fängen war auf den stark beweideten Flächen größer. Bei *Saccostomus campestris* war ein derartiger Unterschied nicht nachweisbar. Die Trockenperiode von 1982/83 führte zu einem Abfall der Populationsdichte von Kleinsäufern im gesamten Untersuchungsgebiet.

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